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COAST LIVE OAK REVEGETATION ON THE CENTRAL COAST OF CALIFORNIA

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ABSTRACT

As part of a revegetation program for *Quercus agrifolia* Nee, we examined the reported effect of nurse plant facilitation on seedling establishment and growth. To investigate this location effect, acorns were planted directly in the ground in 100 positions under shrubs, and in 100 positions in the open. In addition, we tested for the effect of protection by covering half the planting positions with cages. In the first year, acorns planted in the open had higher germination but lower survival than acorns planted under shrubs, resulting in no significant location effect on the success of seedling establishment. The protection effect was significant, with the success of caged seedlings almost double that of uncaged seedlings. After two years, no location effect on seedling survival or growth was found. Cages continued to have a significant positive effect on seedling survival, but they tended to retard their growth. Over five years of monitoring, no significant effect of nurse plant facilitation on seedling survival or growth was found, although the number of seedlings that survived under shrubs was greater than that in the open. We also explored potential relationships of associated vegetation type and crowding on acorn seedling development. Seedling establishment, survival, and growth were associated with differences in vegetation type, and were higher in planting sites with more mesic vegetation. Crowding due to multiple seedlings growing in one planting position versus single seedlings did not negatively affect the growth of seedlings. Of 100 nursery-grown seedlings transplanted in the field in the first year, 99 were surviving at the end of the five-year monitoring period, and on average, they were much larger than the direct acorn plantings. As with the acorn seedlings, no significant nurse plant location effect was found for seedlings transplanted in the open or under shrubs.

Interest in the ecology, recruitment, and revegetation success of *Quercus agrifolia* Nee var. *agrifolia* (coast live oak) in California has heightened in recent years. A primary issue of ecological and conservation concern is that the extent of oak woodland and savanna habitats has decreased due to causes that are not well understood, but may include herbivory, competition, drought stress, cattle grazing, and development. The effects of these factors have been examined for California oaks, particularly *Quercus douglasii* Hook. & Arn. (blue oak) (Griffin 1971, 1976; Muick and Bartolome 1987; Borchert et al. 1989; Davis et al. 1991), but considerably fewer studies have concentrated on *Q. agrifolia.* Since there appears to be a net loss of oak populations statewide, the replacement of oak seedlings has been required as mitigation for development projects that result in the removal of adult oak trees. In many of these projects, the revegetation success with oaks has been poor. To understand fully the reasons for the lack of natural oak recruitment and the limited success of revegetation efforts, long-term studies of 10 or more years would be required; realistically, such long-term studies are seldom possible and systematic data beyond two years are rare.

In a two-year study on coast live oak establishment in Central California, Callaway and D'Antonio (1991) addressed the question of "nurse plant" interactions with *Q. agrifolia* seedling survivorship and found that seedlings grown under shrubs had higher survival rates than seedlings growing in open areas. They suggested that shrubs may reduce environmental stresses on young oak seedlings and provide protection from herbivory. Other researchers found that *Q. agrifolia* seedling survival was facilitated by shade and protection by caging (Muick 1991; Plumb and Hannah 1991).

As part of an environmental mitigation program, the U.S. Air Force was required to compensate for the loss of mature oaks that occurred during the construction of new facilities, roads, and railroads on San Antonio Terrace at Vandenberg Air Force Base (AFB). The project goal was to establish a total of 70 viable *Q. agrifolia* seedlings by the end of the five-year mitigation and monitoring program in 1995. Revegetation was carried out by growing oak seedlings from acorns planted directly in the ground (acorn seedlings), and by transplanting nursery-grown seedlings at the field site (transplant seedlings). We collected survival and growth data consistently over five years for both acorn and transplant seedlings, allowing us to quantify losses that took place during seedling germination and establishment phases. In this paper, we examine the location effect of nurse plant treatments on the survival and growth of the acorn and transplant seedlings. In addition, we investigate the protection effect of caging to explore the role of seed predation/herbivory in the early phases of acorn seedling establishment. Finally, we summarize and compare the survival and growth patterns of all seedlings over five years.

Study site. Vandenberg AFB occupies almost 40,000 ha north of Point Conception on the Central Coast of California. The San Antonio Terrace (34°49′N, 120°35′W) is located in the northern part of the base, between San Antonio Creek to the south and Shuman Creek to the north. The Terrace is ecologically important since much of its area comprises a unique ecosystem of stabilized sand dunes. Dune slopes and ridges are covered by coastal dune scrub vegetation dominated by *Ericameria ericoides* (Less.) Jepson (goldenbush) and *Artemisia californica* Less. (California sagebrush). Many interdune swales contain wetlands that support a number of different plant communities, including a variety of marsh and woodland vegetation types. The woodlands are dominated primarily by *Salix lasiolepis* Benth. (arroyo willow), but in several of the dune swales, *Q. agrifolia* is the dominant canopy species.

The area chosen for the oak revegetation project was located west of Live Oak Springs, a wetland of approximately 2 ha that was created on San Antonio Terrace as part of the environmental mitigation program. The site is within a swale near established oaks. Soils supporting the oaks are sandy, well drained, and have an ample supply of subsurface water. The presence of mature *Q. agrifolia* indicated environmental conditions favorable for the growth of this species; additionally, the shrubby habitat in the area provided some protection for seedlings from browsing animals. No cattle grazing occurs at the site, but *Odocoileus hemionus* (mule deer) and *Sylvilagus bachmani* (brush rabbits) are common in the area, and *Sus scrofa* (feral pigs) are known to be found nearby. Small mammals that prey on acorns, such as *Neotoma fuscipes* (wood rats), *Thomomys bottae* (pocket gophers) and *Spermophilus beecheyi* (ground squirrels), are present at the site, although not in large numbers.

Methods

Planting and field methods. Oak acorns were collected from *Q. agrifolia* on San Antonio Terrace in November and December 1990. To ensure genetic diversity among acorns, several different collection locations were selected. Since live oak acorns require a 30–90 day cold stratification period before they germinate (Schopmeyer 1974), the acorns were stored in a refrigerator until direct planting was carried out in February 1991, during the winter rainy season. Although only 70 seedlings were required for mitigation, many more acorns and seedlings were planted to compensate for: 1) potentially low viability of collected acorns; 2) mortality of seedlings resulting from drought; and 3) potential losses of acorns and seedlings due to herbivory.

Locations for planting were chosen within the elevational zone of occurrence of neighboring mature oaks. For the acorn plantings, 100 locations were chosen under separate shrubs, and 100 locations were chosen about 1 m away from each shrub in open areas. The shrub species used as nurse plants were *E. ericoides, A. californica*, *Baccharis pilularis* DC. (coyote brush), and *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene (western poison oak). A total of 800 acorns were planted, four in a hole at each location, placed sideways just below the surface of the soil. Fifty randomly selected positions from each treatment (shrub/open) were covered with protective cages constructed of hardware cloth (mesh size about 1 cm^2) and shaded with 50 percent shadecloth. Cages were approximately 30 cm in diameter and 45 cm in height. To assure germination and to maintain emerging seedlings, all positions were hand-watered once a week in the initial months after planting, but less frequently thereafter.

Six hundred acorns were sent to a nursery to grow into seedlings. The nursery used a soil mix that included 40 percent sand, 3 percent redwood bark, and peat moss. A slow release fertilizer (19-6-12 nitrogen-potassium-phosphorus) was added, along with small amounts of other nutrients. In addition, a pH buffer of dolomitic lime maintained the mix at a pH of approximately 6 to 6.2 (sandy soils on the Central Coast are generally acidic). The acorns initially were planted in flats. When tap roots of seedlings reached the bottom of the flats, the seedlings were transplanted into 1-gallon containers, where lateral root systems could develop. Transplanting to the 1-gallon containers occurred in April 1991, approximately 60 to 90 days after germination. In November 1991, 100 of 401 available nursery-grown seedlings were transplanted in the field (hereafter referred to as transplant seedlings) at the same site as the acorn seedlings. Approximately half the transplants, chosen randomly, were located under shrubs, and half in open areas (an exact 50-50 split was not possible due to site constraints). Half were protected by cages similar to the acorn plantings, but these transplants were not selected completely at random because some seedlings already were too large to be caged. Due to this size bias, the protection treatment for the transplant seedlings was not analyzed statistically.

As seedlings outgrew the cages, they were removed or replaced by larger cages starting in Summer 1992, and continuing each year. All cages were removed in Fall 1995 at the end of the mitigation program. A drip irrigation system was installed in Fall 1991, with water emitters located at sites where seedlings survived from acorn plantings, and at all transplant locations. The seedlings were watered once per month in drier seasons (June–November). Irrigation ended in fall/winter each year, as soon as normal precipitation began, and was discontinued altogether in Fall 1995 at the end of the mitigation program. Neither the acorn nor the transplant seedlings received any artificial fertilization treatments after planting on San Antonio Terrace. The lack of long-term supplemental water and nutrients was designed to encourage seedlings to adapt to prevailing rainfall conditions and nutrient sources in their natural environment.

Data collection and analysis. Seedling survival was monitored approximately every two weeks in the first four months after acorn seedlings germinated in April 1991, then monthly through August 1992, and then annually through 1995. Transplants were monitored after November 1991 at the same time as the acorn seedlings. Survival data included counting seedlings and documenting their condition. Measurements of height, stem diameter, and leaf number were taken in the summers of 1991, 1992, and 1993 as indicators of growth of surviving acorn seedlings. Only height and stem diameter measurements were taken for transplant seedlings, since measuring leaf number would not have been time-effective. In 1994 and 1995, only height and stem diameter measurements were taken for all seedlings.

Survival and growth data were analyzed using contingency table analysis and two-way analysis of variance (ANOVA) respectively, testing for the effects of location (plantings under nurse shrubs or in the open) and protection (cages present or absent) on the acorn seedlings. Additional factors examined included associated plant species or vegetation type, and the potential effects of crowding due to multiple seedlings growing in a single position. For the transplant seedlings, only the effect of location was examined using ANOVA. Statistical analyses were carried out using CSS:STATISTICA (StatSoft, Inc. 1991).

Results

Acorn seedling germination and survival—Year 1. Using data collected to 18 October 1991, percent germination, seedling survival, and seedling success were assessed for the location and protection treatments. Percent germination refers to the maximum number of acorns (out of the four planted) that germinated at any time. Percent survival is the proportion surviving after germination to a particular time. Percent success is the proportion of planted acorns that germinated and survived (germination multiplied by survival).

The germination, survival, and success data were examined using contingency table analysis. For germination, the effect of location was not statistically significant ($P > 0.05$); the overall mean was 41.8 percent for locations in the open and 33.3 percent for locations under shrubs (Fig. 1a). However, a significant effect of protection was found ($\chi^2 = 16.85$, $P < 0.01$), with a mean germination for caged acorns of 44.3 percent, and a mean of 30.8 percent for acorns without cages (Fig. 1b). Acorn germination stabilized at about the 60th day after first germination; the highest germination occurred for open and caged acorns, the lowest for unprotected acorns planted under shrubs (Fig. 2a).

The survival of acorn seedlings through this period was higher for seedlings that germinated under shrubs than those in the open, but this difference was not significant, with 77.5 percent surviving under shrubs, and 60.9 percent in open areas (Fig. 1a). Caged acorn seedlings survived at a rate almost double that of uncaged acorns; a significant difference, with means of 84.6 percent versus 46.5 percent ($\chi^2 = 26.61$, $P < 0.001$; Fig. 1b).

With respect to the success of acorn plantings, there was no significant effect of location (Fig. 1a), but again, a significant effect for protection was found ($\chi^2 = 39.95$, $P < 0.001$). Mean seedling success was 37.0 percent for caged seedlings and 19.0 percent for uncaged seedlings (Fig. 1b). The higher germination rate for acorns planted in the open was offset by a lower survival rate; and conversely, the lower germination for acorns under shrubs was compensated for by a higher survival rate over time (Fig. 2b). Therefore, overall success was not significantly different between acorn seedlings under shrubs and those in the open. This difference is most apparent when comparing the success of caged seedlings under shrubs and those in the open (Fig. 2c).

In addition to the effects of location and protection, we also examined the potential effect of species of nurse plant on percent germination, survival, and success. The species factor could not be controlled equally due to physical constraints of the planting area, however, the dominant shrub species at each planting location was recorded. Four major shrubs were present: *A. californica, E. ericoides, T. diversilobum*, and *B. pilularis* associated with an understory of *Carex praegracilis* W. Boott (clustered field sedge). Although beneath-shrub sample sizes were not appropriate for robust statistical analysis, a consistent seedling germination-survival-success pattern was observed, with *Baccharis/Carex* sites being followed by planting sites dominated by *Toxicodendron, Ericameria*, and *Artemisia* (Fig. 1c).

To summarize Year 1 results, germination was maximum for caged acorns, particularly in the open, suggesting that these acorns were protected from herbivory and may have received extra soil moisture due to the shadecloth covering the cages; moreover, increased sunlight in open conditions may have facilitated seedling germination. After germination rates leveled off, survival was better for protected seedlings and those under shrubs; protection from above-ground herbivory and good soil moisture retention apparently was provided both by cages and by shrubs. Acorns germinated and seedlings survived better in the *Baccharis/Carex* sites than in sites dominated by other shrub species. The higher success of seedlings in *Baccharis/Carex* sites may reflect higher soil moisture conditions, since these species occupy mesic environments such as wetland swales on the San Antonio Terrace.

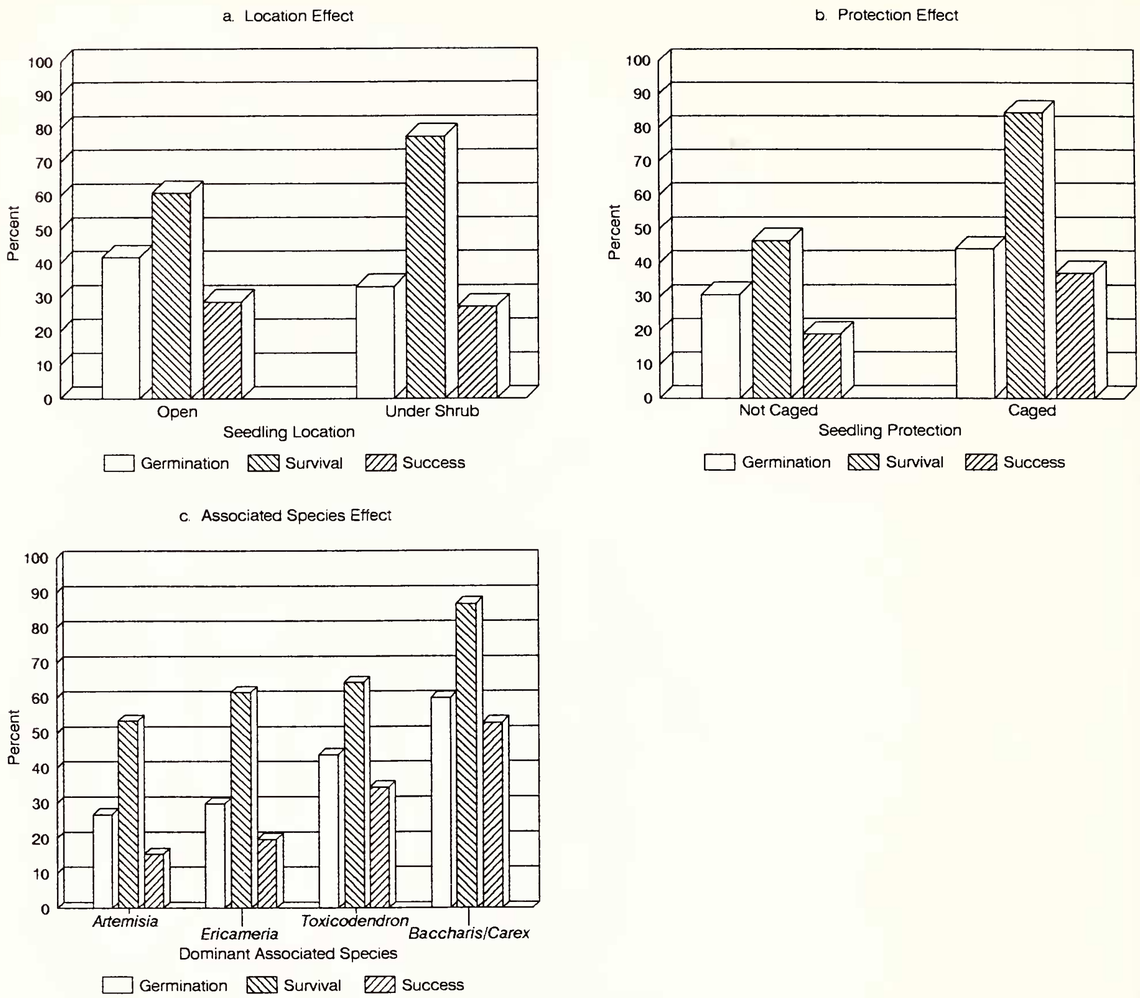

FIG. 1. Percent germination, survival, and success of acorn seedlings from data collected 18 October 1991: the effects of location, protection, and associated species.

Acorn seedling survival and growth—Year 2. At the end of Summer 1992, the effects of location and protection on the number of surviving acorn seedlings and their growth were examined. After this time, the removal of cages from seedlings that outgrew them precluded further experimental testing and analysis of the cage protection effect. The acorn seedlings had been sown in February and germinated by April 1991; therefore, they were approximately 6 months old during first measurements in 1991, and 15 months old during the next period of measurements in 1992, having progressed by then through two growing seasons in the field.

As in Year 1, the effect of the location treatment on seedling success in Year 2 was not found to be significant. With respect to the survival of acorn plantings, 45 positions in the open had live seedlings in 1991, decreasing to 40 in 1992. Under shrubs, 49 positions with live seedlings in 1991 decreased to 43 in 1992. A greater difference in individual seedling mortality was observed, with seedling losses between 1991 and 1992 in the open being three times that under shrubs: 24 of 113 seedlings observed in 1991 were lost in the open, but only 8 of 106 seedlings under shrubs.

The effect of the protection treatment in Year 2 continued to be significant ($\chi^2 = 14.66$, $P < 0.01$). High germination and survival rates for caged positions through 1991 resulted in 146 acorn seedlings, while only 73 survived in uncaged positions. By 1992, seedling survival remained better in caged positions compared to uncaged positions, with 121 seedlings in 54 caged positions versus 66 seedlings in 29 uncaged positions.

ANOVA was used to examine growth measurements taken of acorn seedlings in the first two years. Height and stem diameter of seedlings planted in the open or under shrubs did not show a significant location effect. Likewise, the effect of protection by caging on the growth of acorn seedlings

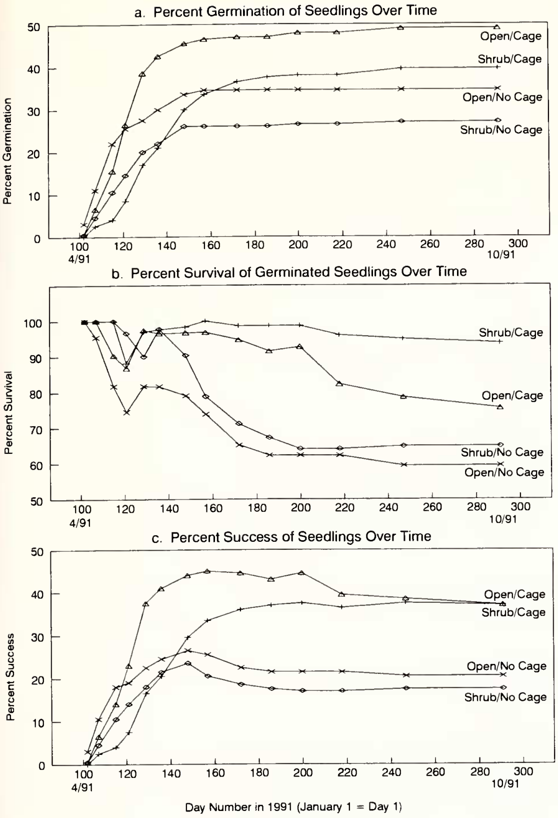

FIG. 2. Percent germination, survival, and success of acorn seedlings with respect to location and protection, April to October 1991.

was not apparent after the first growing season (Figs. 3a and 3b). Subsequently, absolute changes in height and stem diameter were substantially greater for the non-caged seedlings, which doubled in size by 1992. In contrast, the caged seedlings lagged in growth, resulting in a significant difference in both growth parameters for the cage protection effect in 1992 (height: $F_{1,185} = 17.93$, $P < 0.0001$; stem diameter: $F_{1,185} = 23.55$, $P < 0.0001$). The cages apparently tended to retard the growth of seedlings.

For the live acorn seedlings in 1991 and 1992, data were collected on leaf number of seedlings at the same time that the other two growth parameters were measured. In 1991, mean leaf number was 7.34, and by 1992 it was 17.24—an increase of about 135 percent. In both years, the effects of location and protection were significant: leaf number was higher for seedlings located in the open and not caged. For seedlings growing under shrubs or caged, leaf number was lower in both years, likely due to the effect of shading by shrubs or the shadecloth around the cages.

Acorn seedling survival and growth over five years. In early 1991, the mean germination for acorns planted in the field was about 38 percent, yielding 249 seedlings in June, a seedling establishment success of 31 percent. The initial mortality of acorn seedlings was 12.0 percent between June and October 1991. Mortality rates were 14.6 percent between 1991 and 1992; 12.3 percent between 1992 and 1993; 9.8 percent between 1993 and 1994; and 6.8 percent between 1994 and 1995. There were 32, 23, 16, and 10 seedlings lost in these four periods, respectively. By July 1995, 138 live acorn seedlings were recorded (Fig. 4a), a five-year seedling success of 17 percent. Of the 200 planting positions, 72 had at least one live seedling, a success by position of 36 percent.

At various times over the course of the project, the oak seedlings were subject to browsing, mold attacks, woolly oak aphids, leaf mining, and drought stress. These factors apparently resulted in the mortality of acorn seedlings. We also noted in

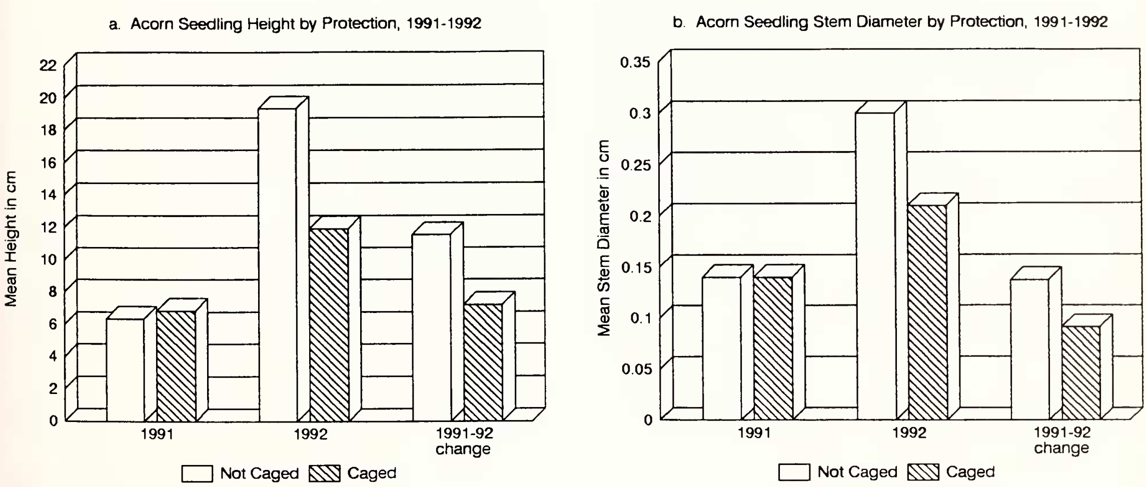

FIG. 3. Growth of acorn seedlings for the protection effect, 1991 to 1992.

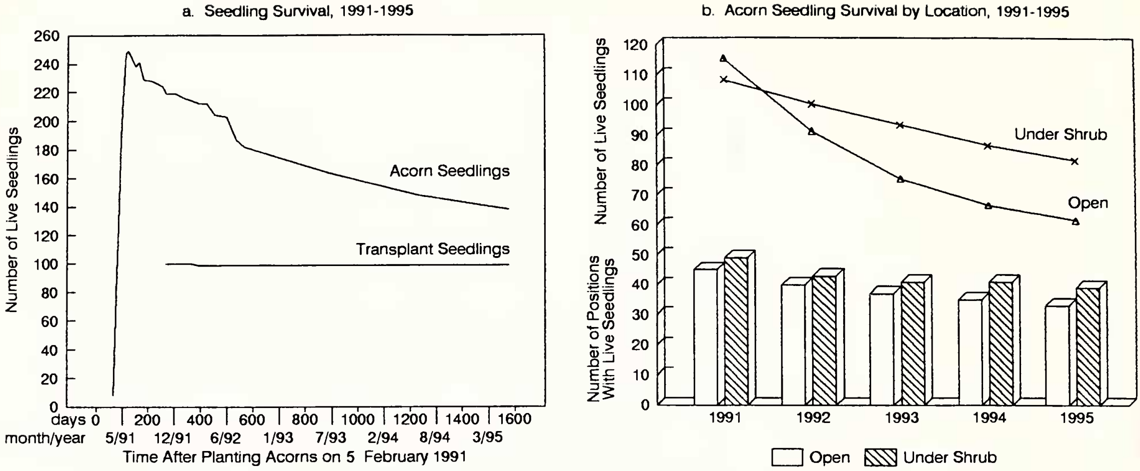

FIG. 4. Seedling survival, and acorn seedling survival by location, 1991 to 1995.

the field that heavy understory cover in the planting positions, both of native and non-native species, tended to have a negative effect on the survival and growth of seedlings in initial years. The understory species probably grew rapidly in response to irrigation of the planting positions in dry months; we observed that clearing the planting positions did appear to facilitate seedling growth, although this factor was not tested experimentally.

With respect to the effect of location on acorn seedling survival, the number of planting positions under shrubs with live seedlings only slightly exceeded the number in the open during the five years of the project. Initially, higher germination led to a greater number of individual seedlings in the open in 1991, but these seedlings suffered higher mortality in later years (Fig. 4b). By 1995, therefore, the absolute number of seedlings surviving under shrubs was greater than that in the open (79 versus 59). This difference, however, was not found to be statistically significant ($\chi^2 = 5.23$, $P > 0.10$).

As discussed previously for the first two years, patterns of acorn seedling growth, analyzed separately each year for years 3 through 5, showed no significant effects of location, with mean height and stem diameter measures being comparable for seedlings growing in the open and under shrubs.

In contrast to the lack of an effect of nurse plant location on the growth of oak seedlings, we observed in the field that acorn seedlings growing in the *Baccharis*/*Carex* sites were considerably larger than those elsewhere. We therefore combined growth and survival data for the planting sites associated with the shrub species *Artemisia, Ericameria*, and *Toxicodendron*, and compared them to data from the *Baccharis*/*Carex* sites. We found that from 1992 onwards, both height and stem diameter were significantly greater for acorn seedlings in the *Baccharis*/*Carex* sites (Figs. 5a and 5b). By 1995, means for height were 33.8 cm versus 55.5 cm for the two vegetation types; and stem diameter means were 0.6 cm versus 1.1 cm (height: $F_{1,136} = 13.42$, $P < 0.001$; stem diameter: $F_{1,136} = 21.80$, $P < 0.0001$).

A further examination of survival of acorn seedlings in the *Baccharis*/*Carex* vegetation type showed that although the number of planting positions and absolute number of live seedlings were smaller in the first two years, these seedlings survived considerably better over the longer term than those planted in the other sites (Fig. 5c). By 1995, the number of positions in each type was similar, but 82 live seedlings survived in the *Baccharis*/*Carex* sites, compared to 56 in the *Artemisia*/*Ericameria*/*Toxicodendron* sites. This finding indicated that more multiple seedlings were present by 1995 in the *Baccharis*/*Carex* sites, while more self-thinning occurred at the other sites.

Acorn seedling self-thinning. The issue of thinning the oak acorn seedlings in reference to positions with multiple seedlings arose while evaluating the revegetation program in later years. To assess for possible crowding effects, survival and growth data were analyzed for the years 1991 to 1995. The number of positions with multiple seedlings decreased over the years, indicating that self-thinning had occurred, particularly where 3 or 4 seedlings were present (Fig. 5d). Analysis of the growth data revealed no significant crowding effects on height or stem diameter over each of the five years, and multiple seedlings (2 to 4) growing in a single position were not significantly different in size than single seedlings. Moreover, no observable differences in health of the single versus multiple seedlings were noted in the field. Therefore, we decided not to thin the seedlings at the end of the monitoring period, and to allow natural mortality to continue.

Transplant seedling survival and growth over five years. Oak seedlings grown in the nursery ger-

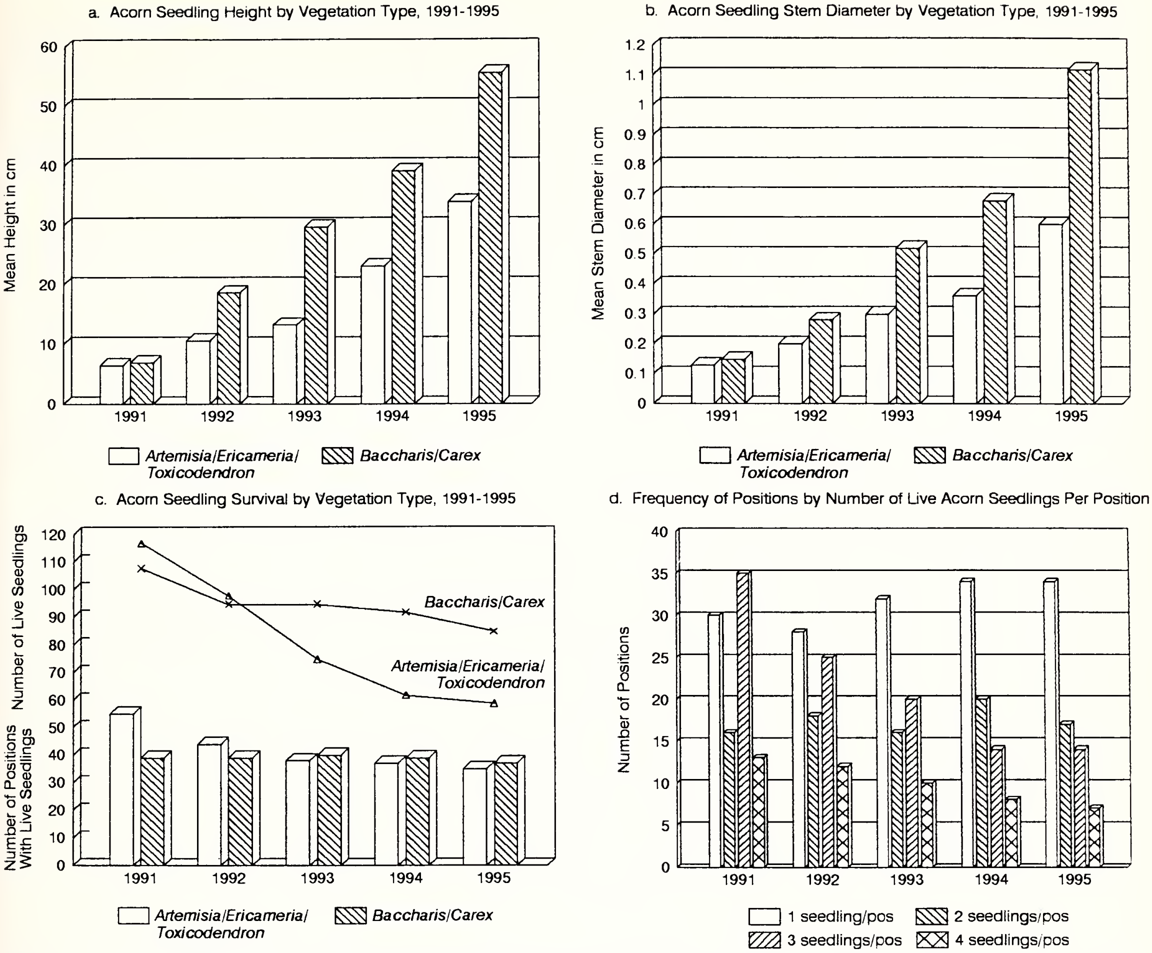

FIG. 5. Acorn seedling growth and survival by vegetation type, and number of acorn seedlings per position, 1991 to 1995.

minated by April 1991, and thus were approximately the same age as the acorn seedlings. One hundred of these seedlings were transplanted in the field in November 1991, after having progressed through one growing season in the nursery. Of the 100 transplants, only one seedling (planted in the open and uncaged) died (in March 1992) throughout the five-year monitoring period (Fig. 4a). Since seedling mortality was negligible, there clearly was no evident effect of location or protection on the survival of transplant seedlings.

By the time the nursery-grown seedlings were transplanted in the field in 1991, they already were much larger than the acorn seedlings. In fact, some of the transplants were too large to be caged, and the protection treatment could not be applied at random, therefore, the effect of caging on growth was not examined. Height and stem diameter measurements were taken at the time of transplanting to provide baseline growth data. In 1991, mean height of transplant seedlings was 45.6 cm and mean stem diameter was 0.81 cm, compared to a mean height of 6.7 cm and a mean stem diameter of 0.14 cm for the acorn seedlings. These two growth parameters were monitored for the transplants and analyzed each year using ANOVA to test for the location treatment, but the results did not show a significant effect for seedlings planted in the open or under shrubs.

Transplant seedlings grew more rapidly and remained much larger than acorn seedlings for all five years. Both height and stem diameter for acorn and transplant seedlings increased dramatically from 1994 to 1995, coinciding with a particularly high rainfall year, when precipitation was almost double the average of the previous four rain years. By the end of the five-year monitoring period in 1995, the mean height of transplant seedlings was 108.8 cm and mean stem diameter was 2.93 cm, compared to a mean height of 46.7 cm and a mean stem diameter of 0.91 cm for the acorn seedlings.

In summary, although it is suggested often that revegetation may be more successful by mimicking natural processes, i.e., favoring the direct planting of acorns in the ground allowing natural root systems to establish, we found that nursery-grown transplants were more successful in the field. They survived at 99 percent and grew on average to more than double the size of directly planted acorn seedlings over five years.

Discussion

The results of this coast live oak revegetation project should be interpreted within the context of the local environmental conditions on the San Antonio Terrace at Vandenberg AFB; the applicability of this study elsewhere would have to be assessed at other sites and in other habitats. Nevertheless, this study raises a number of issues relevant to oak restoration programs in California, and also has implications for future ecological research on the mechanisms of recruitment of this species.

We observed three aspects related to the location effect examining nurse plant facilitation of oak seedlings. 1) Initially, relatively low germination rates but higher survival rates for acorns planted under shrubs led to a similar level of success as that of acorns planted in the open, which germinated at a higher rate but did not survive as well. 2) Over the five years of the project, acorn seedling survival was considerably higher under shrubs, although the difference was not statistically significant. This finding suggests, but does not confirm, that a longer term nurse plant facilitation effect may exist that might not be apparent in early years. 3) With respect to the growth of both acorn and transplant seedlings, their height and stem diameter was not affected by planting positions being located in the open or under shrubs. It appears, rather, that local site factors such as soil moisture, texture, and associated vegetation may have a greater effect on the success and growth of the seedlings. Planting acorns in mesic sites, dominated on the Terrace by *Baccharis/Carex* vegetation was more successful with significantly greater growth than planting in drier sites, even though large healthy oak trees were present very close to the planting positions in the drier sites and all sites were irrigated equally. This finding may partially explain the remarkable success of nursery-grown seedlings which were transplanted primarily to the *Baccharis/Carex* area.

Regarding the protection of acorns planted directly in the ground, caging in the initial months appears to facilitate both germination and survival of seedlings, therefore leading to higher initial success. However, in the second year of the program, the cages tended to retard the growth of the seedlings, indicating that they should be constructed to be larger in size from the beginning, or that they should be removed as soon as seedlings begin to outgrow the cages.

We also found that crowding of seedlings due to germination of multiple acorns planted in one position did not affect the growth of seedlings, and that self-thinning did occur at the scale of individual planting positions. Longer-term monitoring would help to assess the progress of multiple seedlings at this scale, as well as to examine the density and distribution of revegetated oaks at the larger site scale as seedlings grow into the sapling and tree stages. Such monitoring would enable the investigation of larger scale growth and thinning processes and the evaluation of optimum spacing between surviving healthy plants.

Our findings are consistent with field observations (Griffin 1973) as well as experimental results (Callaway 1990), which indicate that *Q. agrifolia* tends to be scarce in drier habitats, due in part to its dependence on lateral root systems that acquire moisture from the upper layers of the soil. In addition to its relatively short roots, Matsuda and McBride (1986, 1987) suggest that the distribution of *Q. agrifolia* in mesic sites is related to its slower germination and a larger leaf area to root weight ratio than other California oaks. In general, we found that although there appears to be some nurse plant facilitation of oak seedling survival, if not growth, other key factors related to microsite variations, particularly soil moisture, may be more important in affecting both seedling survival and growth. The effect of associated vegetation type that we observed may reflect a complex of ecological variables including those related to topography, geology, and hydrology, such as slope, aspect, elevation, soil texture, chemistry, nutrients, and moisture. More research and experimental investigation over greater periods of time than five years is needed to evaluate these factors.

Acknowledgments

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